FIGS. 37 and 38.—Two stages of segmentation mitoses.

FIGS. 39 to 48 represent eggs of the spring generation.

FIG. 39 *a*, *b*.—Two successive sections of chromosome group at edge of egg before maturation division.

FIG. 40.—Early stage of maturation division.

FIG. 41.—Late stage of maturation division.

FIG. 42.—Completion of maturation division. Chromosomes of egg-nucleus sinking in; polar chromosomes in two groups.

FIG. 43 *a*, *b*, *c*.—Polar chromosomes and egg-nucleus. *a* and *b*, successive sections of polar chromosomes; *c*, egg nucleus several sections removed. (× about 800.)

FIG. 44 *a*, *b*.—Two equatorial plates of segmentation mitoses, showing about 20 chromosomes.

FIG. 45.—Prophase of segmentation mitosis, showing numerous long coiled chromosomes.

FIG. 46 *a*, *b*, *c*.—Metaphase (*a*), early (*b*), and late anaphases (*c*) of normal segmentation mitoses with diploid number.

FIG. 47.—Equatorial plate in face of segmentation mitosis with haploid number.

FIG. 48 *a*, *b*, *c*.—Metaphase (*a*), anaphase (*b*) in side view, and anaphase in pole view (*c*) of segmentation mitoses with haploid number.

Preliminary Note upon the Cell Lamination of the Cerebral Cortex of Echidna, with an Enumeration of the Fibres in the Cranial Nerves.

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(Communicated by Dr. F. W. Mott, F.R.S. Received September 30,—Read December 9, 1909.)

[PLATES 4 AND 5.]

Material.—The following notes are based on the study of the brain of an Echidna which died in the gardens of the Zoological Society in London.

Dr. F. W. Mott, F.R.S., kindly placed the brain in my hands with the suggestion that I should examine the cell lamination of the cortex and should estimate the numbers of fibres in the cranial nerves. For this and for his advice and help during the investigation I wish here to express my gratitude.

The right hemisphere was cut transversely into a series of sections 10 μ in thickness, from which sections were taken at intervals of about $\frac{1}{2}$ mm., stained with polychrome blue, and mounted. It may, perhaps, be mentioned

that the sections were somewhat erratic in their behaviour towards the stain, and required a prolonged immersion in it. The preservation of the cells was not sufficiently good to justify any minute histological description, and therefore none such has been attempted, nor has the large variety of cell outlines been described. A great deal of this apparent diversity must be due to the cutting of similar cells in slightly different planes, and to the many aspects which cells of the same type must present to the observer according as they are placed in this position or that. Moreover, it was felt that the drawings (figs. 3, 4, 5, 6) in which the cells are represented in silhouette display both their shape and their arrangement more clearly and more briefly than could any verbal description.

Owing to the general shape of the hemisphere and, more particularly in its posterior part, to the course of the fissures, transverse sections in the neighbourhood of the two extremities are confusing on account of the obliquity with which the cortex is cut. In order to obviate this difficulty sections were cut from the left hemisphere in such a way that they met the fissures as much as possible at right angles. In spite of this it has not been found possible to give any adequate presentment of the cortex at the anterior and posterior extremities of the brain, but it is hoped to obtain fresh material with which the gaps in the present paper may be filled up.

Ziehen* gives descriptions of certain types of cortex to be found in the brain of Echidna but no figures either of the cell lamination or to explain in what part of the hemisphere the structures he describes may be found. As I could not from his verbal descriptions get any clear notion on the latter point, I have omitted to compare his descriptions with my own.

Surface Anatomy of the Brain (*vide* fig. 1).

Before beginning a study of the transverse sections, in order that these may be understood, it may be as well to say something of the arrangement of the fissures. The latter have been described by G. Elliot Smith† and by Ziehen.‡ The descriptions agree in all essentials, but whereas Elliot Smith designates the different fissures by letters of the Greek alphabet, Ziehen provides them with long Latin names indicating their positions on the brain.

* "Das Central-Nerven-System der Monotremen und Marsupialer," 2. Theil, Microscopische Anatomie; 'Jenaische Denkschr.,' VI, 2. Theil; Semon, 'Zoolog. Forschungsreisen,' III, 2. Theil, p. 848.

† Museum of the Royal College of Surgeons of England, Catalogue of Physiological Series, vol. 2, second edition, 1902.

‡ "Das Central-Nerven-System der Monotremen und Marsupialer," Semon, 'Zoolog. Forschungsreisen,' III, p. 8; 'Jenaische Denkschriften,' VI.

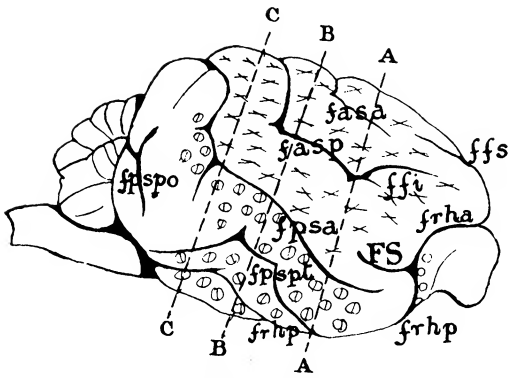

FIG. 1.—A.

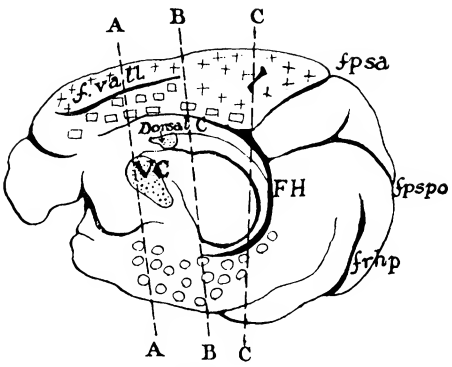

FIG. 1.—B.

FIG. 1.—Diagram of right hemisphere of Echidna. ×2½. A, Lateral aspect; B, Median aspect.

Fissures.

FS	Fissura Sylvii.	*fasa*	Fissura antesylvia anterior.
frha	„ rhinica posterior.	*ffs*	„ frontomarginalis superior.
frhp	„ rhinica anterior.	*ffi*	„ frontomarginalis inferior.
fpsa	„ postsylvia anterior.	*FH*.....	„ hippocampi.
fpspo	„ postsylvia posterior occipitalis.	*Fvall*	„ vallaris.
fpspt	„ postsylvia posterior temporalis.	*VC*	Anterior (ventral) commissure.
fasp	„ antesylvia posterior.	*Dorsal C*...	Dorsal commissure.

A - - - *A* shows plane of Section *A*.
B - - - *B* „ „ *B*.
C - - - *C* „ „ *C*.

Types of Cortex.

□ □ □ ..... Type I.
\+ + + + ... Type II.
× × × × ..... Type III.
◐ ◐ ◐ ◐ ..... Type IV.
○ ○ ○ ○ ..... Type V.

Ziehen's names, though clumsy, have the advantage that they remind one of the position of the fissure referred to, and it is for this reason that they are adopted here.

He takes as his starting point the—

Fissura Sylvii (*FS*).—This is generally about 5 mm. in length, and runs almost horizontally backwards. From its anterior end the fissura rhinica anterior runs forwards and the fissura rhinica posterior runs backwards.

Fissura rhinica anterior (*frha*) runs horizontally forwards and reaches the mesial surface. Its incision of the mantle edge delimits the olfactory lobe

or bulb. The greatest depth of the fissure is 7 or 8 mm., but the incision referred to is 9 mm. deep.

Fissura rhinica posterior (*frhp*) runs at first basalwards, then turns horizontally backwards, and describes finally a flat curve with its concavity directed downwards. Its posterior segment, sometimes separated from the main division, cuts the posterior mesial border of the hemisphere. The depth in the anterior division is about 7 mm., but gets considerably less posteriorly.

Fissura postsylvia anterior (*fpsa*) [Elliot Smith, α] approaches the sylvian fissure at its lower end in a characteristic manner; it runs upwards and backwards and cuts the mesial border of the hemisphere 25 mm. from the frontal pole. It may be straight or wavy, but there is always an angular bend in the middle third from which a posteriorly directed side branch is given off. The depth is between $2\frac{1}{2}$ and $4\frac{1}{2}$ mm.

Fissura postsylvia posterior (*fpsp*) lies 6 mm. behind *fpsa*; it cuts the border of the hemisphere behind the occipital pole, *i.e.* behind the point where the border runs laterally outwards. The fissure runs continuously downwards and forwards as far as the angle of *fpsa*, but in front of this its direction is continued by an anterior segment. The main fissure is called f. postsylvia posterior occipitalis (*fpspo*) [Elliot Smith, ζ], and is $2\frac{1}{2}$ mm. deep. The anterior segment is called f. postsylvia posterior temporalis (*fpspt*) [Elliot Smith, η], and is $1\frac{1}{2}$ mm. deep. Occasionally another fissure, f. postsylvia postrema, is present behind and parallel to *fpsp*.

Fissura antesylvia posterior (*fasp*) [Elliot Smith, β] is the most constant of the fissures in the anterior part of the brain; it lies parallel to *fpsa*, 2 to 6 mm. in front of it. When well developed its lower end lies over the sylvian fissure. In this region it often turns sagitally forwards and may be forked. Its depth may reach 3 mm. Between it and *fpsa* there may be another fissure.

Fissura antesylvia anterior (*fasa*) [Elliot Smith, γ and δ) lies parallel to and in front of *fasp*. It is sometimes as well developed as the latter, and cuts deeply into the mesial border of the hemisphere. More often it is weakly developed, failing to reach the border and sometimes falling into two pieces. Its lower end may be forked, depth to 3 mm.

Fissuræ frontomarginales superior and inferior (*ffs* and *ffi*) [Elliot Smith, ϵ] lie in front of *fasa*; they are very variable.

On the median surface of the brain may be found the *Fissura hippocampi* (*FH*) which follows the characteristic course of the hippocampus, starting in the upper anterior part of the brain, running backwards and then curving downwards and finally forwards, to end somewhere below its starting point.

Fissura vallaris (*f vall*) runs parallel to the border of the hemisphere in the anterior part of the brain. Its length is about 10 mm. Its posterior end lies above the anterior commissure, its anterior end 5 to 6 mm. from the frontal pole.

Radial Fissures.—Three or four may be present, of which the anterior may be a median prolongation of *fasa*. The second is sometimes independent, sometimes a prolongation of *fasp*. The third is generally very sharply defined, and is always in continuity with *fpsa*; it may have the appearance of being connected with *FH*. The fourth is often very weak and is usually independent.

Elliot Smith says that the fissure ψ is the deepest and most constant of the radiating sulci in the mesial surface of the brain. In most brains it crosses the dorsal edge and joins β (*fasp*) in the dorsal surface.

Description of Five Distinct Types of Cell Lamination, with Notes as to Their Distribution.

The sections A, B, and C, diagrammatically represented in fig. 2, are intended to illustrate the distribution of the various types of cortex in the middle region of the hemisphere. The position of these sections which are cut transversely is shown in fig. 1. This figure also shows the distribution of the types of cortex on the surface of the brain. From it and from the foregoing descriptions the manner in which the various fissures are cut may be understood.

Type I. □ □.

This cortex measures only 1 mm. in depth, and is not very highly differentiated. The molecular layer occupies rather less than 0·1 mm. It is succeeded by a layer of broad and irregular rectangular or pyramidal cells, which stretch downwards to a depth of 0·5 mm. While in the upper region of this layer the cells are small (15 to 20 μ in length), they become considerably larger (20 to 27 μ) in the neighbourhood of its lower boundary, and are there more regular in shape and arrangement. The rest of the cortex is made up of small polymorphic cells. A few granules are found in the polymorphic layer and in the lower part of the pyramidal layer.

Type I may be found in the median wall of the hemisphere, lying between the *Fissura vallaris* (*F vall*) and the *Fissura hippocampi* (*FH*). It extends backwards some way behind the posterior end of the former. It may be seen in practically the same position in sections A, B, and C. In section A the Hippocampal fissure is quite shallow, but posterior to this it gets much deeper, and as it deepens the cortex originally lying above it becomes invaginated so as to clothe its upper wall.

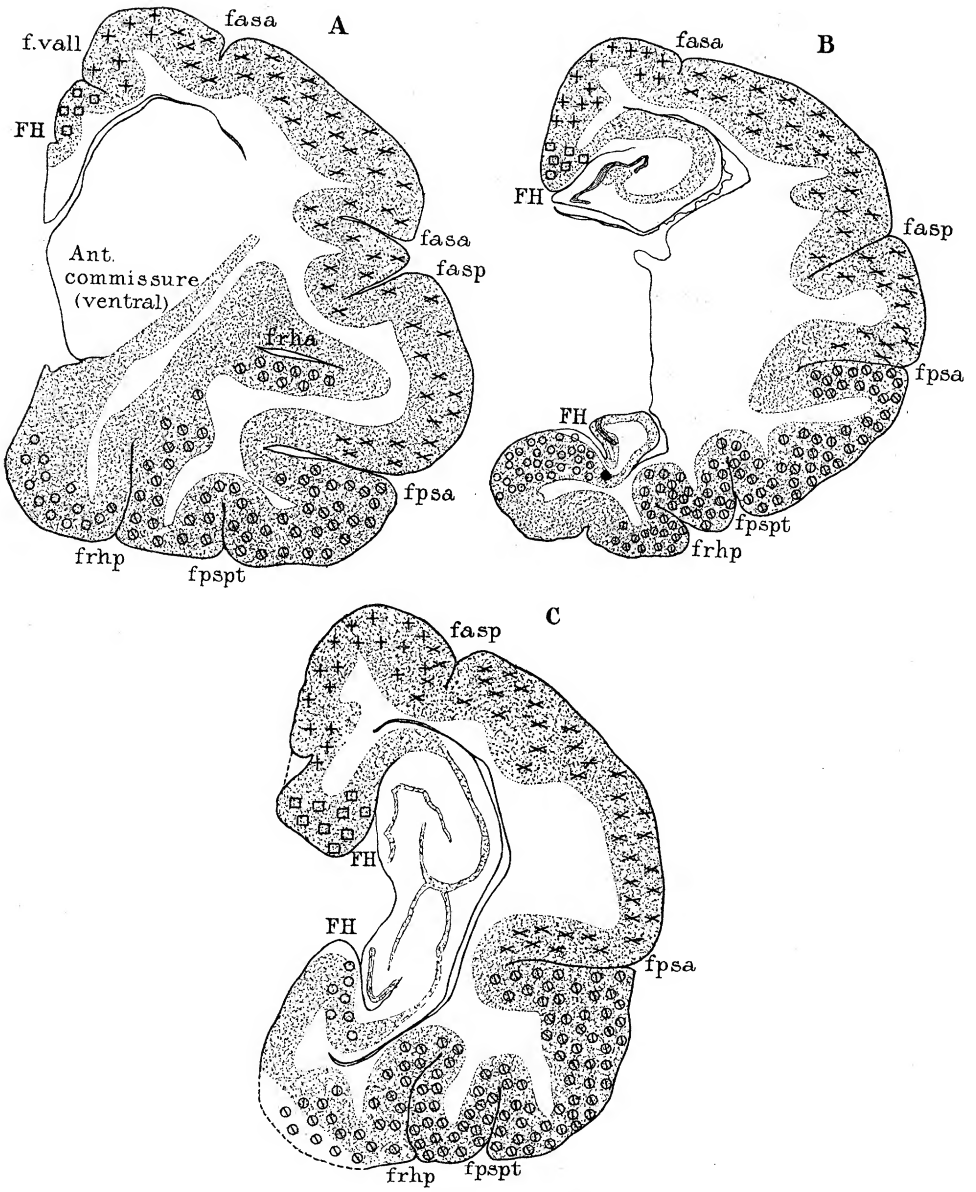

FIG. 2.—Transverse sections of right hemisphere. $\times 5\frac{1}{4}$. (For position of sections and lettering *vide* fig. 1.)

TYPE II. + + + (*vide* fig. 3).

Fig. 3 is drawn from the superomesial border. The depth of cortex is here about 1·5 mm. The following layers can be distinguished:—

1. Molecular layer, depth 0·05 mm.

2. A superficial layer of somewhat closely-packed cells of irregular shapes, characterised by being broad relative to their length. The size of these is about 8 to 18 μ in length and 7 to 12 μ in breadth. About 0·1 mm. from the surface the cells begin to get less crowded, and at a depth of 0·2 mm. a layer (3), somewhat poor in cells, succeeds. This is about 0·25 mm. broad. What cells are contained in it seem a shade larger than those of layer 2, and they become larger as one goes deeper. They are somewhat irregular in shape, but many are roughly pyramidal.

4. Layer of large pyramids starts 0·5 mm. from the surface and stretches downwards to a depth of 0·9 mm. The majority of the cells in this layer are elongated and somewhat irregular pyramids measuring up to 30 μ in length and 15 μ in breadth, with an average size of 25 × 10 μ or so. Their nuclei are 7 × 13 μ or somewhat less. Among these large characteristic cells, which are present in considerable numbers, lie many much smaller cells. These granules extend throughout the cortex except in the most superficial portion, but they are most numerous among and immediately below the large pyramids.

5. The rest of the cortex is made up of small polymorphic and spindle-shaped cells measuring about 25 × 8 μ, with roundish nuclei 5·7 μ in diameter.

Distribution.—Type II may be found on the mesial surface of the hemisphere dorsal to the fissura vallaris. Anteriorly it extends at least as far as that fissure, while posteriorly its limit appears to be the radial fissure continuous with fissura postsylvia anterior (*fpsa*). Above it spreads over the superomesial border on to the lateral surface, where it abuts on the area covered by Type III.

Type III. × × × (*vide* fig. 4).

Fig. 4 is drawn from a strip on the lateral surface about 5 mm. from the superomesial border, and 3 mm. from the point at which Type II changes into Type III. The depth of the cortex is here about 1·75 mm.

The following layers may be recognised:—

1. *Molecular.*—0·13 mm. in breadth, or more than double the breadth of the molecular layer of Type II.

2. Layer of "small pyramids" somewhat elongated in shape, measuring 12 to 30 μ in length × 5 to 10 μ in breadth.

Although some might correctly be described as pyramids, the majority are not pyramidal, but rather sausage- or spindle-shaped. They often have two apical processes. This layer extends to a depth of about 0·4 mm.

3. A zone about 0·5 mm. in breadth rather poorer in cells than layer 2.

The cells are some of them irregular pyramids slightly larger than in that layer, while others are smaller cells of the granule type. The latter are to be met with also in the deeper layers, but are more numerous here.

4. Layer of large pyramids about 0·4 mm. in breadth.

The cells are much the same as those of the corresponding portion of Type II; they lie 0·4 mm. farther from the surface.

5. Layer of polymorphic cells. This is about three-quarters of the breadth of the corresponding layer in Type II, measuring 0·45 mm. across. The constituent cells of both types appear to be much the same in structure.

Distribution.—This type of cortex covers the greater part of the lateral surface of the hemisphere. Above it changes more or less suddenly into Type II; below and behind the fissura postsylvia anterior (*fpsa*) forms its boundary, while in front it extends almost as far as the fissura rhinica anterior (*frha*). It is separated from the upper lip of that fissure by a narrow strip of cortex of simple structure, rather resembling Type I Type III varies somewhat in its details in different parts of the wide area which it covers. It is narrower on the walls of the fissures, the cells are less numerous and are shorter and broader.

TYPE IV. ⓘ ⓘ ⓘ ⓘ (*vide* fig. 5).

The depth of cortex is about 1·8 mm. The following layers may be distinguished:—

1. Molecular layer, 0·2 mm. deep.

2. Dense layer of cells of various shapes, measuring 15 to 30 μ in length. There are some pyramidal, giving off one process towards the surface, while others are inverted pyramids giving off two or more processes in that direction; others again are stellate or fusiform. This layer stretches to a depth of 0·5 mm. In its deeper portion, the cells are less crowded, and a number of granules are present.

3. A distinct layer of granules, 0·3 mm. in width, which stretches to a depth of 0·8 mm. The exact shape of the granules was difficult to determine owing to bad preservation. Among them are larger cells of pyramidal or irregular shape.

4. A layer of large pyramids and polymorphic cells, of which many are 30 to 35 μ in length. Among them are smaller cells of the same shapes and scattered granules. This layer has no very definite boundary, but its constituents get smaller at a depth of about 1·1 mm.

TYPE V. ○○○○ (*vide* fig. 6).

1. The molecular layer is very broad, stretching downwards to depth of 0·4 mm. below the surface.

2. A dense layer of large, darkly staining cells, measuring up to $35 \times 20\ \mu$. These cells are characterised by the strong development of their dendrites, two of which are often directed towards the surface.

3. At 0·6 mm. below the surface, or just above, these cells give place to others, distinguished from them by being slightly smaller and irregularly pyramidal or pyriform in shape, with only one apical process. This layer extends downwards to depth of rather less than 0·9 mm.

4. A stratum almost devoid of cells, about 0·1 mm. broad.

5. At a depth of 1 mm. a layer of polymorphic cells may be found, which measure about $20 \times 15\ \mu$. Cells of this type occur throughout the rest of the cortex, but at a depth of 1·2 mm. they become less numerous and are partly replaced by numbers of small stellate cells.

6. Thus a sixth layer can be distinguished, characterised by the presence of the latter. It stretches from 1·2 to 1·6 mm. from the surface.

Distribution of Cortex of Type IV and Type V.

Cortex of Type IV may be seen in Section A, lying between the fissura rhinica posterior (*frhp*) and the fissura postsylvia anterior (*fpsa*). In this section the fissura rhinica anterior (*frha*) is cut in a plane more or less parallel to the direction in which it runs but at right angles to its walls. The walls are thus shown in section near to the bottom of the fissure. It will be seen that the cell lamination of the lower wall is of Type IV. In a section taken a little in front of this the whole length of *frha* is cut in this way and the fissure is shown opening on to the lateral surface of the hemisphere, but in such a section the lower wall is made up, at any rate near its outer end, of cortex of Type V. In Section A the latter type of cortex is seen lying on the mesial side of *frhp*. In this region and anterior to it, it is of a slightly different structure to that illustrated in fig. 6, which was taken from Section B. The cells of the outer layer are smaller, not so numerous, nor so rich in dendrites. In Section B it will be seen that Type V has left the region of *frhp* and only covers the part of the rhinencephalon lying next to the hippocampal fissure (*FH*). Meanwhile Type IV has encroached beyond *frhp*, which in Section A formed the boundary between the two types. Types IV and V do not pass directly into one another, but are separated by a broad strip of cortex more or less intermediate in structure. This lacks the most characteristic feature of each of the two types which it separates, namely the layer of granules of the one and the large, darkly staining cells in the outer layer of the other. The latter do not stop suddenly nor die out gradually, but they become first reduced in numbers, then arranged in groups separated by free spaces and then finally disappear.

In Section C the same general arrangement is seen, but the strip of Type V has become narrower and of Type IV broader. In Sections A, B, and C the upper boundary of Type IV is formed by *fpsa*. A short way behind Section C this fissure changes its direction, running more vertically upwards. Cortex of Type IV runs upwards as a narrow tongue behind it.

The Numbers of Nerve Fibres in the Cranial Nerves of Echidna.

It was suggested to me by Dr. Mott that the numbers of fibres in the cranial nerves might offer a useful indication of the relative development of different parts of the cerebrum, and consequently the piece of work described here was undertaken.

The material available was the brain from which the foregoing description of the cerebral cortex was made, and a brain of *Echidna setosa* which had been brought back by Mr. Geoffrey Smith from Tasmania. The latter was not in a good enough state of preservation to be used for any other purpose but the counting of the fibres in the cranial nerves.

Nerves III, IV, VI, VII, IX, X, XI, XII were small enough to be viewed in one field of the microscope under a magnification great enough to see each fibre in the stained transverse section separately, or, when not small enough, they were divided into separate nerve bundles, each of which could be viewed as a whole. The counting of the fibres was in these cases a simple and direct, though somewhat laborious matter. A plan was made of each nerve by means of the "Abbé" drawing apparatus, a dot or circle representing each nerve fibre. The dots or circles were then carefully counted.

Nerves II, V, and VIII were too large in transverse section to be treated in this way, and were not conveniently divided up by connective tissue. Another method had therefore to be adopted. The transverse section of the nerve was placed under a power just low enough for it to be entirely included in the field of the microscope, and its outline was traced by means of the drawing apparatus. Then, without shifting the paper or drawing apparatus, or changing the lenses of the microscope, a Zeiss object netz-micrometer was substituted for the microscope slide bearing the section, and the small squares ruled on this apparatus were traced on the top of the drawing. Each of these squares has sides 1/20 mm. in length, and therefore an area of 1/400 sq. mm. By counting the number of squares included in the outline of the nerve, a fairly accurate estimate of the area of the transverse section can be obtained, which is not in any way affected by the distortion produced by the camera lucida.

A sufficiently high power was then put on the microscope and the outline of a convenient number of squares traced on a fresh piece of paper; the

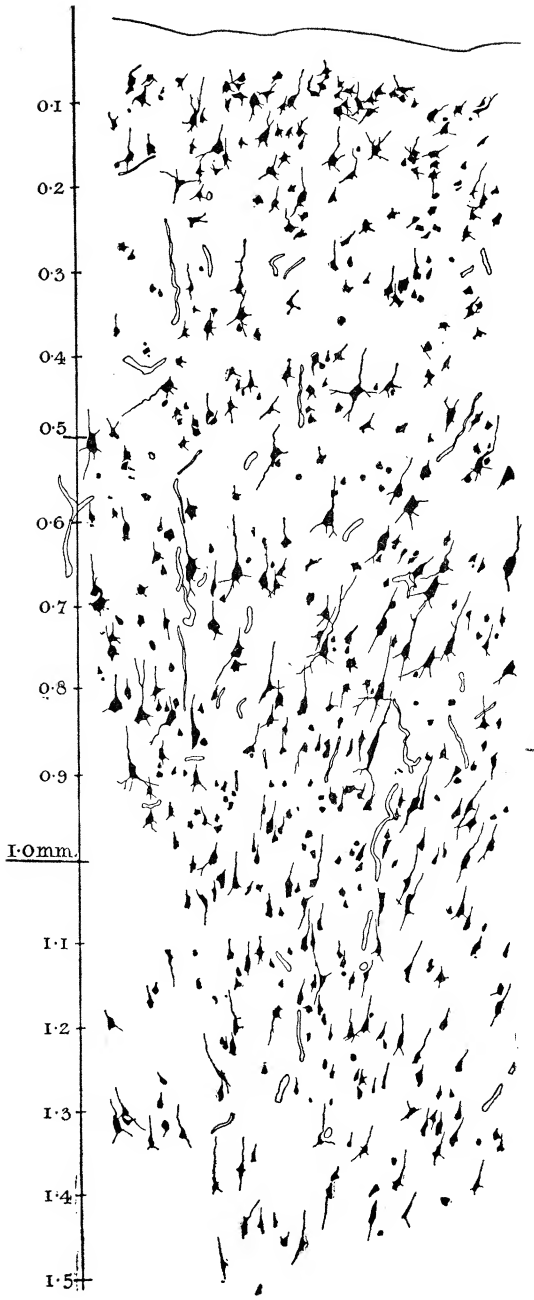

FIG. 3.—(Type 2) × 190.

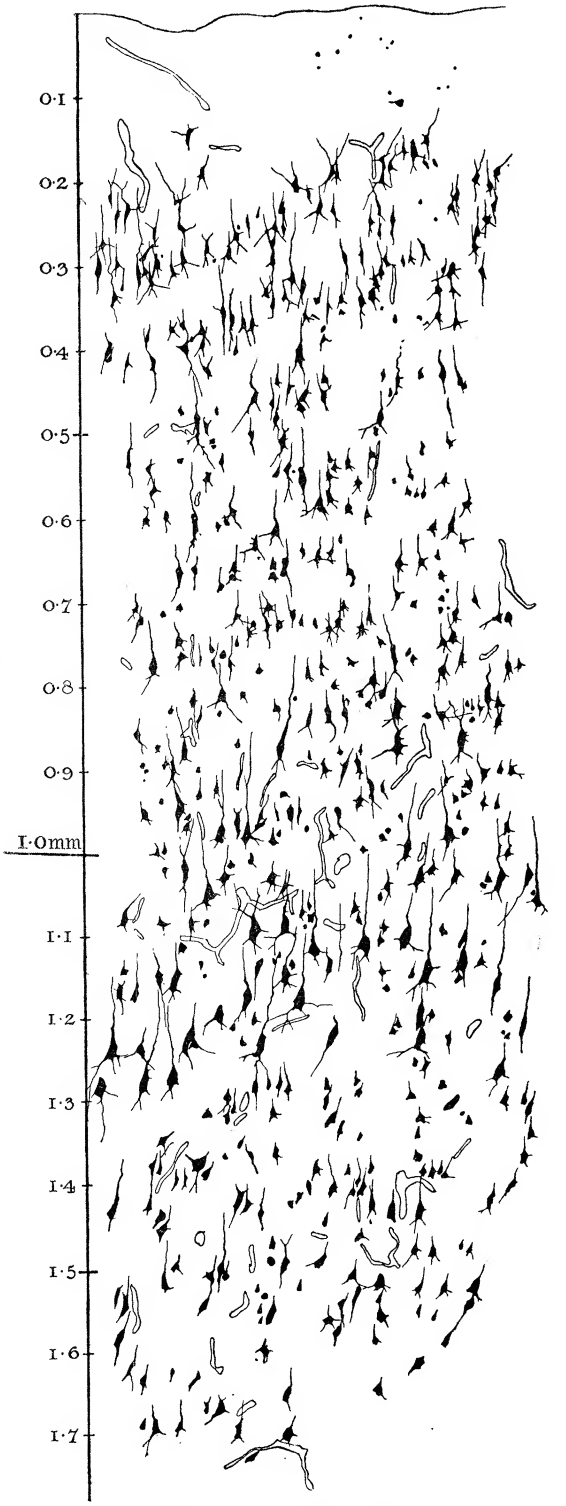

FIG. 4.—(Type 3) × 190.

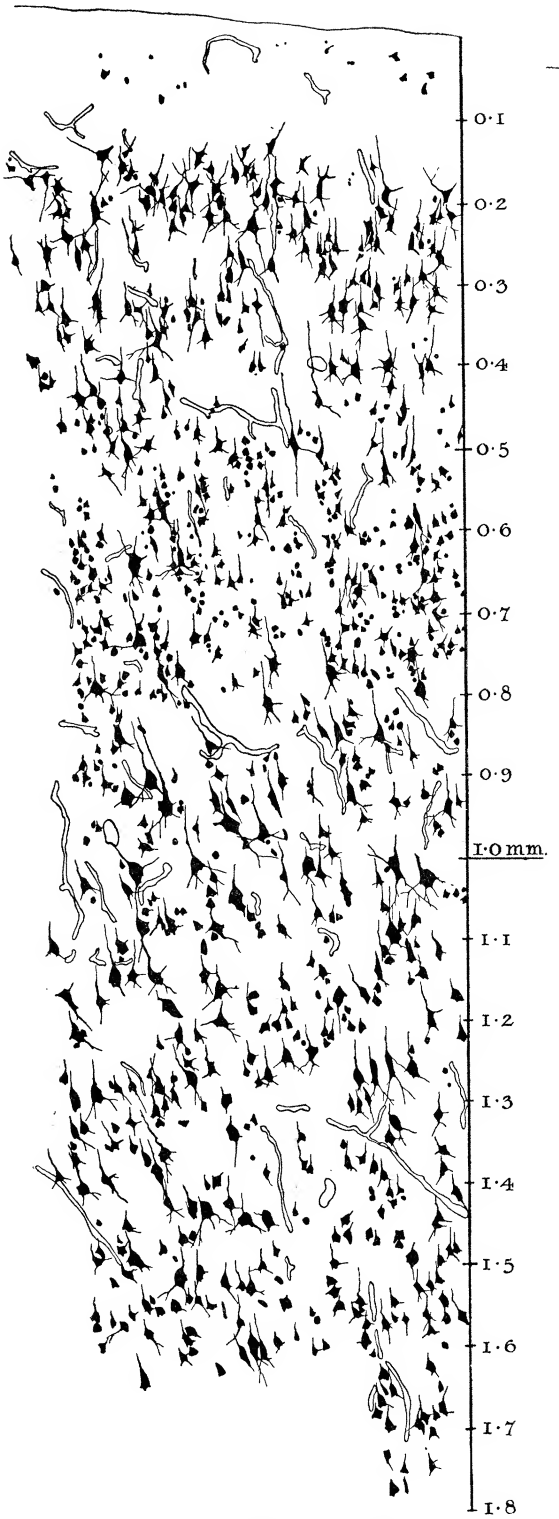

FIG. 5.—(Type 4) × 190.

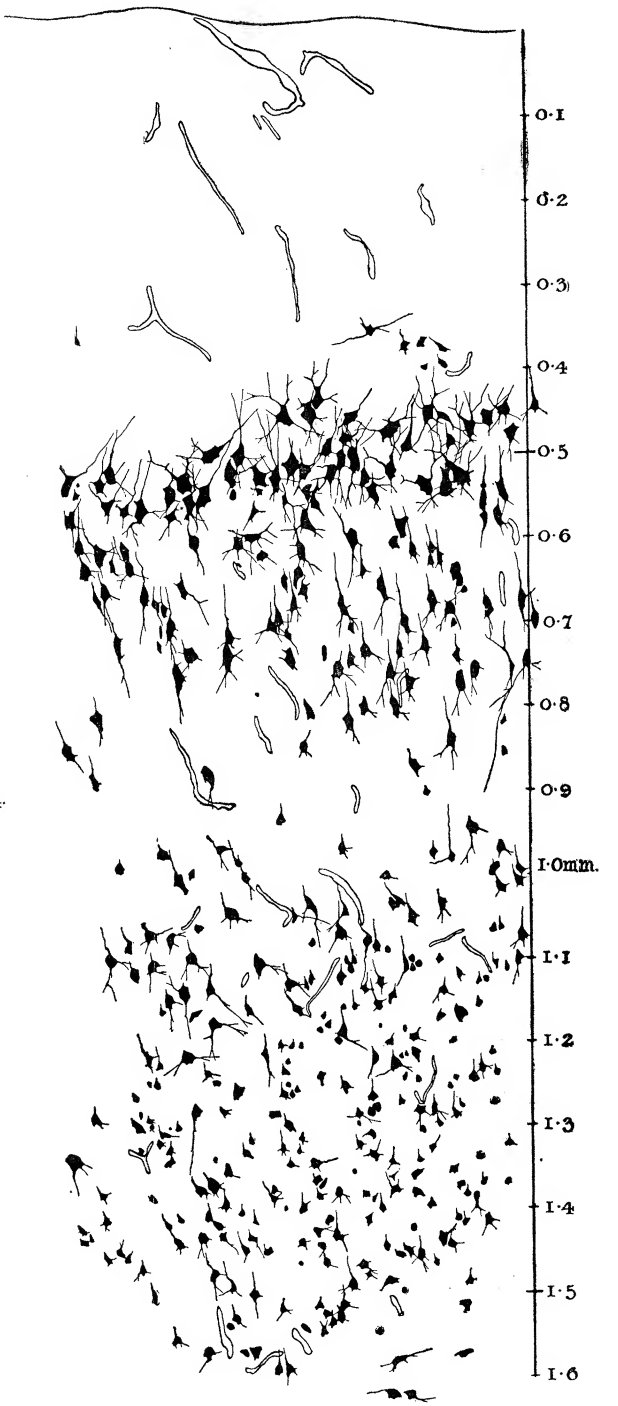

FIG. 6.—(Type 5) × 190.

section was then substituted for the micrometer and all the fibres lying within the outline of the squares were marked. Thus the number of fibres in a definite area of the section was ascertained. This was done two or three times in different parts of the nerve. By dividing the total area of the nerve by the area for which the number of nerve fibres is known and multiplying by the latter number, an estimate of the total number of fibres in the nerve may be obtained, the accuracy of which will vary with the ratio of the known to the unknown, and with the degree of uniformity with which the fibres are scattered throughout the nerve.

The following is a concrete example, namely the optic nerve in Series A :—

Under the low power (16 mm. appochr. obj., 8 comp. occ.), its area was found to be 0·295 sq. mm. The number of nerve fibres for 0·01 sq. mm. was found by the high power (2 mm. appochr. imm. obj., 4 comp. occ.) to be in three different places 974, 942, 992, respectively, which have an average 969.

$$969 \times 0{\cdot}295 \div 0{\cdot}01 = 28{,}585.$$

The results obtained by these two methods are summarised in the table.

Table showing Number of Nerve Fibres in the Cranial Nerves of two Specimens of Echidna.

Nerve.	Brain A.	Brain B.
II	28,585*	46,566*
III	1,978	1,849
IV	404	223
V	—†	43,410*
VI	671	474
VII	4,281	3,535
VIII	24,565*	23,523*
IX	2,740	2,170
X	3,617	3,042
XI	3,227	2,180
XII	5,214	2,865

A, Echidna from Zoological Gardens. B, *Echidna setosa* from Tasmania.

* Number estimated by the method described in text.

† Owing to there having been only a very short piece of the Vth nerve in Specimen A available for sectionising, which was about as long as it was broad, it was accidentally cut longitudinally and not transversely, and was thus useless for the purpose of counting the fibres.